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Carbohydrate and Nutrient Content in Rhizomes of *Phragmites australis* from Different Habitats of Lake Fertõ/Neusiedlersee

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With 14 Figures and 2 Tables

Key words: Rhizomes, carbohydrate, nutrient concentration, standing stock, vigorous reed, die-back reed

Abstract

Changes in the soluble sugar, starch, total non-structural carbohydrate (TNC) and nutrient (N, P, K) concentration in the reed rhizome were investigated in different reed habitat types in Lake Fertõ/Neusiedlersee during the vegetation period in 1993 to 94. Three die-back and four vigorous reed stands were monitored.

For biomass estimations rhizomes were collected twice, in early summer and in autumn. They were calculated to be 1.9 to 2.7 kg/m^2 at die-back and 3.1 to 6.1 kg/m^2 at vigorous sites.

The carbohydrate and nutrient concentrations of the reed rhizomes were high at the beginning of the vegetation period; they reached their minima in May-June, which was followed by a gradual increase until the end of the vegetation period. From autumn to spring the concentrations decreased, e.g. TNC concentration by 15 to 40% at vigorous, 50 to 70% at die-back sites.

In both years the lowest carbohydrate concentrations were recorded at the end of May, a month before the inflorescence developed (vigorous sites: 50–70 mg TNC/g, die-back sites: 70–120 mg TNC/g). In that period the standing stock of the TNC in the rhizome did not separate the sites clearly, and the smallest carbohydrate standing stock was measured at a vigorous site with a high water cover.

At the beginning of summer and in autumn the soluble sugar, TNC and N concentration values were higher at the die-back than at the vigorous sites but the standing stock was higher at the vigorous sites. In autumn the TNC standing stock of the rhizomes was between 780 and 1200 g/m^2 at vigorous, between 380 and 690 g/m^2 at die-back sites. This is especially important for the reactions and resistance of die-back reed stands to unfavourable conditions.

1. Introduction

Reed degradation is a large-scale process in Europe (HARTOG et al. 1989; OSTENDORP 1989). Several characteristics of this phenomenon have been described. Shoot density could decrease (HIRSHER 1987; RAGHI-ATRI & BORNKAMM 1979) or just the opposite, increase but together with the production of weaker, thinner shoots in degrading reeds. The structure of the reed stand often changes, it becomes thin (OSTENDORP 1990) and in many cases the degrading stands are also shorter than the vigorous ones (DINKA 1986; BOAR et al. 1989; KOVÁCS 1990).

Reed is a perennial plant and its survival and spreading greatly depends on the functioning of the rhizome system (CHAPIN et al. 1990; ČIŽKOVÁ-KONČALOVA et al. 1992). This is the reason why the amount and dynamics of the different nutrients and non-structural carbohydrates in the rhizome are very important (DYKYJOVÁ & HRADECKÁ 1976; HO 1981; BRÄNDLE 1985; DINKA 1986; HALDEMANN & BRÄNDLE 1986).

Structural changes and phenological differences occur together with metabolic differences. The amount of stored nutrients, first of all non-structural carbohydrate and the element content, is different in degrading and in vigorous reed stands (ČIŽKOVA et al. 1995; WOITKE et al. 1995).

One of the aims of our project, the subject of this article, is the study of the carbohydrate and the nutrient content changes of the rhizome during the vegetation period in degrading and vigorous reed stands.

Our research hypothesis was that the carbohydrate pool development and utilization has basically similar dynamics in vigorous and degrading reed stands, but the amount of the stored carbohydrate differs. The nutrient accumulation and utilization during the vegetation period was also considered to be similar in the two reed stand types, unlike the intensity of nutrient cycling.

2. Sampling sites

Lake Fertõ/Neusiedlersee (Fig. 1, Table 1) is the largest sodic-lake in Europe, a biosphere reserve declared by UNESCO in 1977 to 1979.

Four vigorous and three die-back sites were selected (Fig. 1) in the 86% reed covered, 75 km^2 Hungarian part of Lake Fertõ/Neusiedlersee on the basis of aerial photos and field observations (MÁRKUS 1983).

The meteorological data were collected at an open-water station (Fig. 1) 30 m from the reed belt (water depth around 100 cm).

Table 1. Fundamental characteristics of Lake Fertõ/Neusiedlersee.

	Surface	Open Water	Reed stands	
	[km^2]	[area km^2]	[km^2]	[% of lake surface]
Austria	234	124.0	110.0	47
Hungary	75	11.4	63.6	86
Total	309	135.4	173.6	56

Mean water depth: 110 cm
Latitude: 47°37′ – 47°57′ N
Longitude: 16°41′ – 16°52′ E

2.1. Sites with vigorous reed (numbers refer to Fig. 1)

- Sampling site 2: Dense, non harvested stand. The caterpillars of *Laelia cenosa* greatly damaged the leaf blades in 1993. Associated species: *Typha angustifolia*. The habitat is flooded only in spring, later the water level sinks below the mud layer. Sedimentation is weak. The area was burned in February of 1994.
- Sampling site 4: Vigorous, annually cut reed stand. Slight damage caused by insects was detected. The habitat is flooded only in spring. Associated species: *Typha angustifolia*. Damage caused by harvesting machines during the winter of 1994 was also recorded.
- Sampling site 5: A homogenous stand with aggregated reed growth. It is situated on the eastern side of the greatest inner lake of the Hungarian reed belt, where the water is deep (100–150 cm). *Laelia cenosa* strongly damaged the leaves in early summer, 1993.
- Sampling site 9: Dense, harvested, vigorous stand, with 10 to 20 cm water cover in spring months. It turned dry in summer, 1993. *Typha angustifolia* sporadically occurs there. In 1994 there was a permanent 5 to 10 cm water cover all round year at all three sites due to a high water level (rainy year).

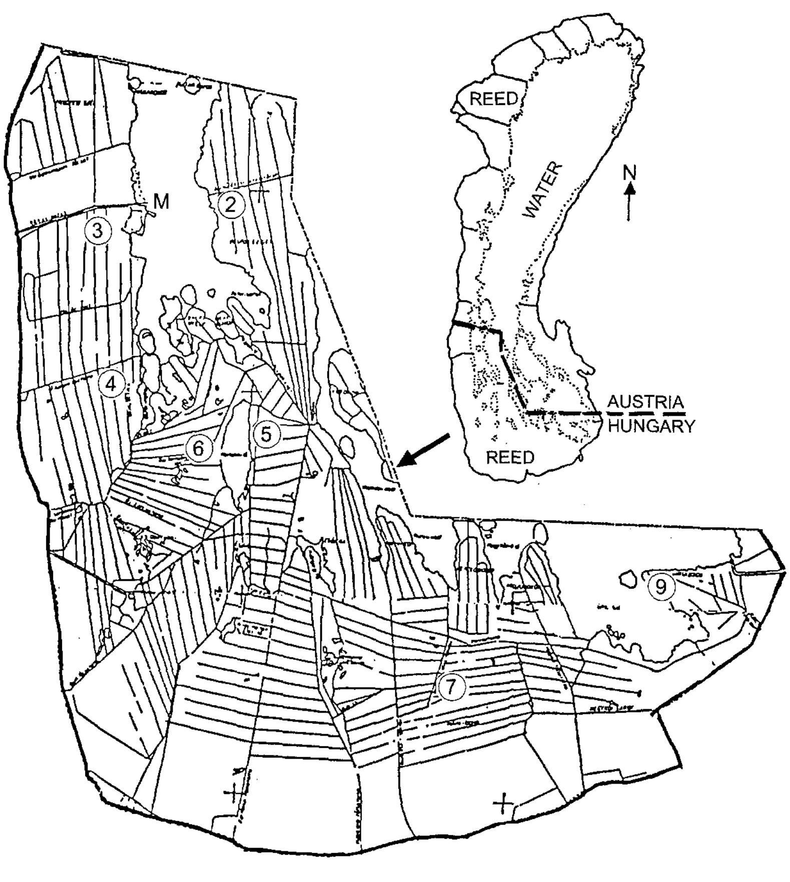


Fig. 1. Sampling sites in Lake Fertõ/Neusiedlersee. M: Meteorological Station. Vigorous sites: No. 2, 4, 5 and 9; die-back sites: No. 3, 6 and 7.

2.2. Die-back sites (numbers refer to Fig. 1)

Reed occurs in clumps of different sizes. In general the open water area is larger than the reed covered surface at these sites. The stands have not been harvested for a long time, but they had previously been destroyed by harvesters.

- Sampling site 3: There are dense stands of *Chara foetida* and *Ch. crinita* in the water bodies, the organic mud layer is deep. The habitat is flooded all year and only the higher reed tussocks become dry in summer. Strong damage caused by insects (*Lipara lucens*) was observed in the early summer of 1993.
- Sampling site 6: The number of dead, destroyed culms is more or less equal to that of the vigorous ones. Insect damage was recognized in the summer of 1993. Associated species: *Typha angustifolia.*
- Sampling site 7: Because of former harvesting damage, few inflorescences developed in the reed stand. Associated species: *Typha angustifolia* occurs sporadically.

There is a permanent 30 to 50 cm water cover at all the three sites. The rhizomes have smaller diameters at the die-back sites than at the vigorous ones. 30 to 50% of the rhizome mass was decayed or decaying here, only one to two years old vertical rhizomes could be collected from these sites. Similar samples were taken from the vigorous sites for comparison.

3. Material and Method

Reed rhizome samples were collected monthly from April to October in 1993 and from March to October in 1994 to measure their carbohydrate and nutrient concentrations. Additional samples were collected to determine the biomass of the rhizomes at the beginning of summer and in autumn.

Sampling was carried out with a 1 m long, 19.5 cm diameter PVC tube. The core drill was pushed into the rhizome system, the upper end was closed and then the sampler was pulled out. The created vacuum ensured the extraction of the rhizomes in the tube (SHIERUP 1978) even from the depth of 70 cm. Three samples were taken from each sampling site. 85 to 90% of the rhizome below 70 cm was decayed.

The rhizome was separated for healthy, decaying and decayed parts. A necessary amount from the healthy parts (one to two years old vertical rhizomes, including both internodium and nodus) were frozen with dry ice in the field. In the laboratory samples were dried at 40 °C, ground and homogenized. Data are given in dry mass.

Soluble sugar was extracted from 250 mg of ground material with ethanol and determined photometrically. Glucose was used as a standard. The unsoluble remainder was resolved in perchloric acid. The starch concentration was determined by using the colour reaction of anthron dissolved in sulphuric acid measured at 630 nm with a Contiflo Automatic Current Analyzer (MCCREADY et al. 1950; SMITH 1969; CONTIFLO 1982; ČIŽKOVÁ & KVĚT 1993). The total nonstructural carbohydrate (TNC) concentration was defined as the sum of the soluble sugar and starch concentrations. The sugar and starch concentrations were measured twice from each sample.

The N and P contents were determined photometrically from the solution obtained from the organs by wet combustion with strong sulphuric acid (in the presence of Se catalyst) using the CONTIFLO Automatic Current Analyzer (HÁMORINÉ 1959; GYŐRI 1973). In the resulting solution, the total N was determined with the indophenol-blue method (640 nm), the P with the molybdene method (400 nm). From the same solution the K concentration was determined by flame-photometry.

Analysis of variance was used to evaluate statistically the results (SVÁB 1979) by the Statgraf 1.0 for Windows program package. Mean values were compared on the basis of the significance of the smallest differences, confidence limits are also given. The mean values of the parameters are plotted, together with their 95% confidence limits. This way significant differences can also be seen in the figures.

Biomass, sugar, starch, N, P and K standing stock per unit (1 m^2) was calculated from the dry mass of the live rhizome and the concentrations of the above mentioned compounds. Two typical standing stock values of the vegetation period were calculated, when it was the lowest (May 26, 1993) and the highest (October 24, 1994).

The first was selected to represent that part of the life cycle, when the nutrient and carbohydrate reserves of the rhizome are used up, the second indicates the most intensive reserve building period.

4. Results

4.1. Changes during the vegetation period

- Meteorology

The following facts describe the meteorological and hydrological differences between the two investigated years: The water level of Lake Fertő/Neusiedlersee was higher during the complete period of study in 1994 than in 1993 (Fig. 2). It meant an important stress by increasing the energy needs first of all at site 5, where the water is deep, and at the die-back sites under permanent water cover especially in early spring.

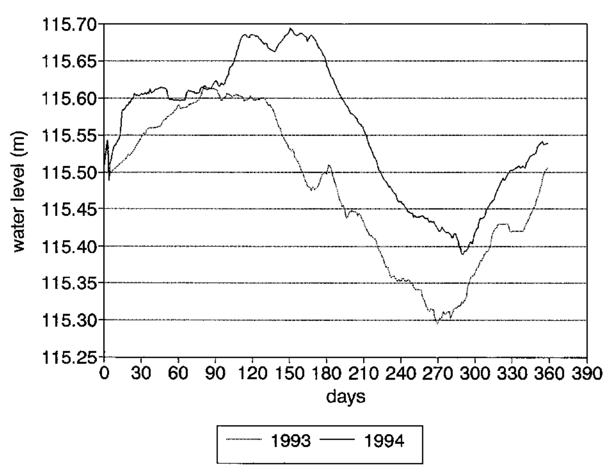


Fig. 2. Water level above the Adriatic Sea level in Lake Fertő/Neusiedlersee in 1993 and 1994.

Besides the high water level, the temperature was also higher in 1994 than in 1993 with e.g. a 5 to 7 °C higher daily average air temperature in early spring at the beginning of shoot development (Fig. 3).

The temperature of the sediment surface in the open water part of the lake closely followed the daily average air temperature, and the high sediment temperature in early spring was favourable for the shoot development of reed (Fig. 4).

• Carbohydrate

Fig. 5 demonstrates the carbohydrate concentration changes at vigorous and die-back sites during the vegetation period.

The TNC values dropped from the early spring concentrations (170–220 mg/g) to minima by the beginning of summer, when shoot development is the most intensive and shoot density reaches a 60 to 70% limit. The lowest TNC concentrations were 50 to 70 mg/g at vigorous sites, 70 to 120 mg/g at die-back sites. In the second part of the vegetation period TNC reserves were built up in the rhizome reaching a maximum concentration (250–350 mg/g) by the end of inflorescence development in August (240th day). From September to October the TNC concentration decreased in the investigated part by 20 to 30 mg/g due to translocation into older rhizomes (FIALA 1976; ČIŽKOVÁ et al. 1995) and the formation of the new lateral shoots (KÜHL & KOHL 1992). 90 to 95% of the assimilating leaf surface dies off during this period (BURIAN 1971).

Similar tendencies characterized the soluble sugar concentration changes during the vegetation period in 1993 and 1994 (Fig. 5). The relatively high early spring concentrations (vigorous sites: 120–150 mg/g; die-back sites: 100–120 mg/g) decreased to their minima in May (vigorous sites: 10–50 mg/g; die-back sites: 38–85 mg/g). Later they increased again with the intensity of the assimilation processes. At the end of the vegetation period the soluble sugar concentration was similar or higher than in spring and it decreased to a limited extent from autumn to spring during the dormancy of reed (Table 2).

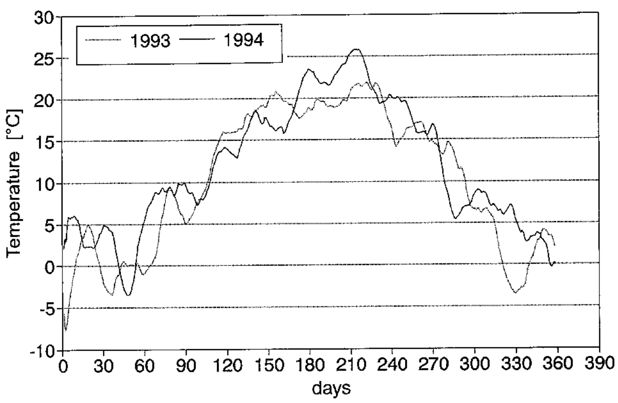


Fig. 3. Main daily air temperature at Lake Fertõ/Neusiedlersee in 1993 and 1994.

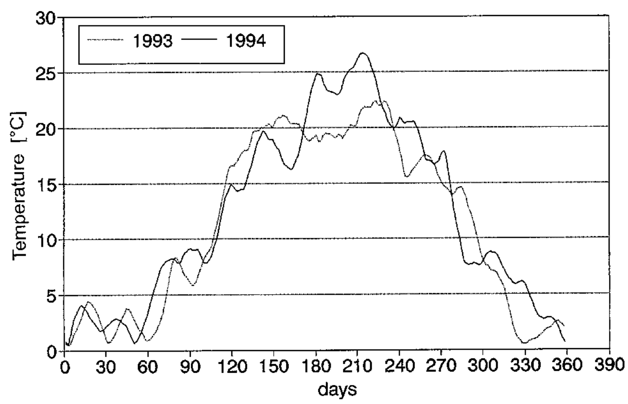
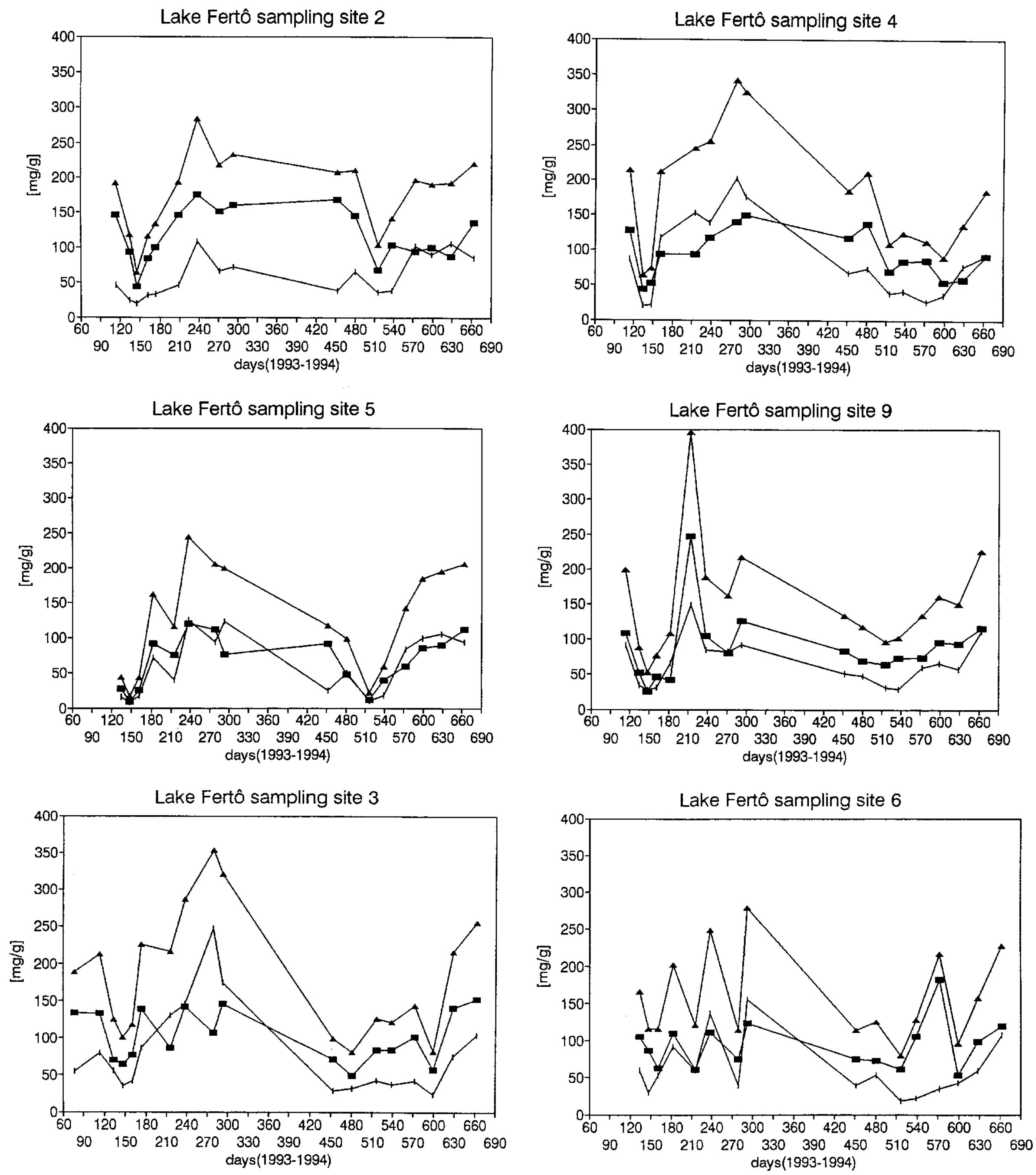


Fig. 4. Temperature of the sediment surface at 8 a.m. in Lake Fertõ/Neusiedlersee in 1993 and 1994.

Table 2. Changes in the carbohydrate and nutrient concentration from autumn to spring (October 23, 1993–March 13, 1994).

Sites	TNC [%]	Soluble sugar [%]	Starch [%]	N [%]	P [%]	K [%]	Shoot* [%]
Vigorous							
2	–14.56	–4.14	–40.90	–41.51	–88.60	14.30	16.67
4	–43.50	–29.64	–54.93	26.93	–38.93	–37.41	79.14
5	–43.90	19.01	–85.36	–31.53	–83.09	0.00	56.43
9	–42.30	–36.07	–52.54	–35.62	–70.41	7.81	42.44
Die-back							
3	–69.00	–56.79	–79.83	77.83	–83.21	–59.93	49.48
6	–58.50	–31.35	–76.89	–49.83	–83.67	–54.14	36.08
7	–50.60	–16.03	–83.62	–4.21	–76.52	26.10	25.72

* Relative number of shoots on March 23, 1994 expressed as the percentage of the maximal shoot number on August, 1994



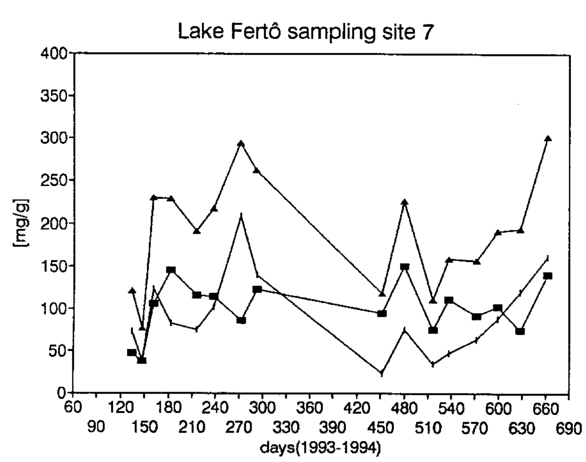


Fig. 5. Changes in the non-structural carbohydrate (TNC) concentration of rhizomes in Lake Fertõ/Neusiedlersee. Vigorous sites: No. 2, 4, 5 and 9; die-back sites: No. 3, 6 and 7.

Explanations: –■– soluble sugar; –+– starch; –▲– TNC.

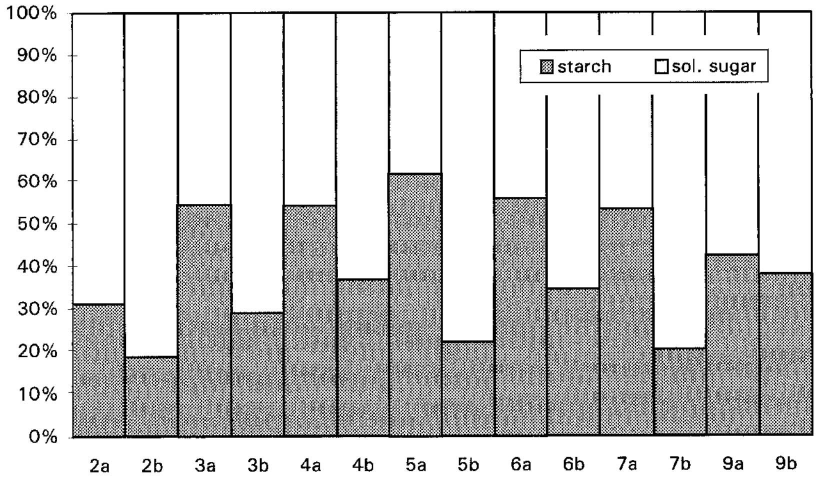


Fig. 6. Percentage distribution of soluble sugar and starch among the sampling sites. Explanations: No. with (a) = autumn (Oktober 10, 1993); No. with (b) = spring (March 29, 1994).

The starch concentration changed similarly in the vegetation period of the two investigated years (Fig. 5). It varied between 50 and 90 mg/g at vigorous sites, between 50 and 60 mg/g at die-back sites. It uniformly decreased at all sites in the first part of the vegetation period (down to 25–40 mg/g, which were the lowest values during the year, see Fig. 5). From May to October it increased again reaching 1.5 to 2 (sites 2, 4 and 9) or even 3 times (sites 3 and 7) higher values than in spring. There was a sharp decline in the starch concentration between the investigated years from autumn to spring at all sites (see Table 2, Fig. 5). KUBIN et al. (1994) detected a starch concentration decrease first of all in eutrophic reeds, while WOITKE et al. (1995) measured a TNC concentration increase. In the latter case the soluble sugar-starch ratio was considerably shifted towards a larger amount of sugar from autumn to spring similarly to our results, but we found a general TNC concentration decrease from autumn to spring (Fig. 6). The carbohydrate and nutrient concentration difference was used up for respiration, bud formation and very slow growth. Similarly to 1993, in 1994 it was the lowest at the end of May again from autumn to spring after it had increased in March and April in 1994 (450th–480th day) due to the mobilization of carbohydrates from two to three year old, older rhizome parts (FIALA 1976; GRANÉLI et al. 1983; KUBIN et al. 1994; ČIŽKOVÁ et al. 1995).

• Nutrients

There were no important differences in the fluctuation of the N, P and K concentrations of the rhizomes between the individual sampling sites during the two years. Fig. 7 shows the changes at two vigorous (No. 2 and 5) and two die-back (No. 3 and 6) sites. Spatial differences are discussed in chapter 4.2.

The N concentration decreased from April. The lowest values were recorded at the end of May (vigorous sites) or in August (site 6). From September to the end of October the N concentration was equal to, or higher than that of early spring. From October to March it decreased (Fig. 7, Table 2) until the next vegetation period. During the whole period of study the N concentrations at site 5 were about 50% of the other values.

The P concentrations decreased from spring to July and increased again in the second part of the vegetation period (Fig. 7).

The K concentration was recorded until March, 1994. It decreased from a high early spring concentration until May, which was followed by an increase until June to July and a second minimum in August. Then it increased during the last phase of the vegetation period (Fig. 7). It did not change at the vigorous sites (2 and 5) but greatly decreased at the die-back sites (3 and 6) (see Fig. 7 and Table 2) between the two vegetation periods from autumn to spring.

4.2. Comparison of the sampling sites

Analysis of variance was carried out using all data to compare the sites on the basis of the investigated parameters. Only those selected results which best distinguish the sites are discussed here. As a result the period of the early summer minima (May 26, 1993) and the end of the vegetation period (October 24, 1994), when storage processes practically finished, are described in detail. Spring values (May 26, 1993) are symbolised by 'I' (near the y axis), autumn ones (October 24, 1994) by 'II' in Figs. 8 to 14. At all sites two means (I, II) with the least significant differences are given.

• Concentrations

Fig. 8 shows differences between the sites according to their soluble sugar concentrations. This way spatial as well as temporal differences can be compared at the same time.

In early spring the significantly smallest values were measured at site 5, in a vigorous reed stand. Significant differences were recorded between the soluble sugar concentration of all the other sites too (with the exception of sites 2 and 7). The highest values were recorded at two die-back sites

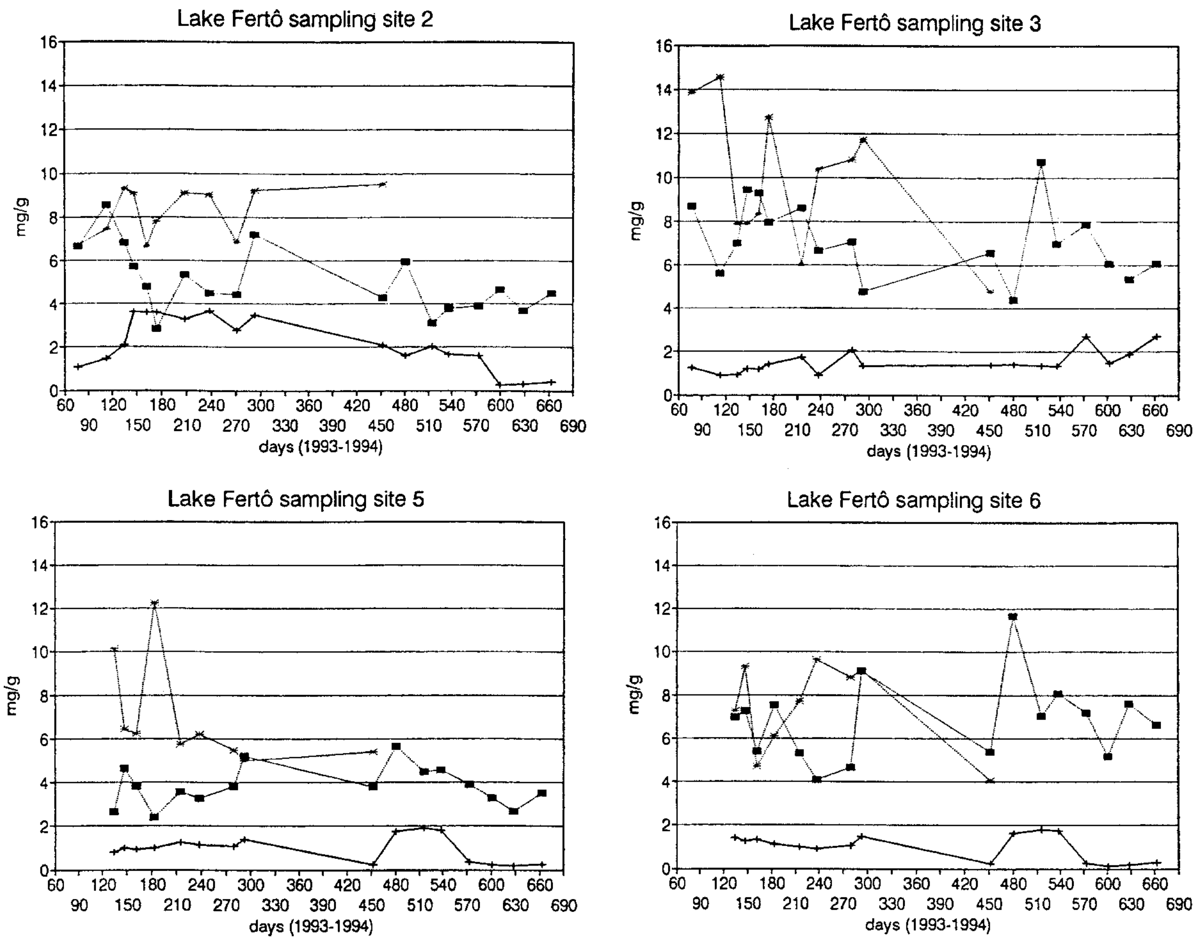


Fig. 7. Changes in the nutrient content of the rhizomes at Lake Fertõ/Neusiedlersee. Vigorous sites: No. 2 and 5; die-back sites: No. 3 and 6. Explanations: ∗–∗ K; -■- N; +–+ P.

(No. 3 and 6). In October, at the end of the vegetation period the concentration of soluble sugars in the rhizomes increased (see Fig. 5). It was still the smallest at two vigorous, and the highest at two die-back sites (No. 4 and 5, No. 3 and 7, respectively).

No considerable difference was found in the starch concentration of the rhizome between the sites in summer, when it was the lowest (Fig. 9). In autumn there was only one site (No. 7, a die-back reed) where significantly high values were measured, all the other values were similar to each other.

There were significant differences between the TNC concentrations of the sampling sites (Fig. 10). As with the sugar concentration, it was the lowest at site 5 in early summer. In autumn it was the highest at sites 3 and 7 (two die-back sites) and the lowest at sites 4 and 5 (two vigorous sites). The first and the latter two sites also differed significantly from each other.

The lowest nutrient (N, P and K) and carbohydrate concentrations were measured in different months (see Figs. 5, 6 and 7). A comparison of the sampling sites on the basis of their nutrient concentrations is also given here for the same period.

The N concentration was significantly high at sites 3 and 6 (die-back sites). It was significantly lowest at sites 4 and 5 (vigorous sites) both in early summer and autumn (Fig. 11).

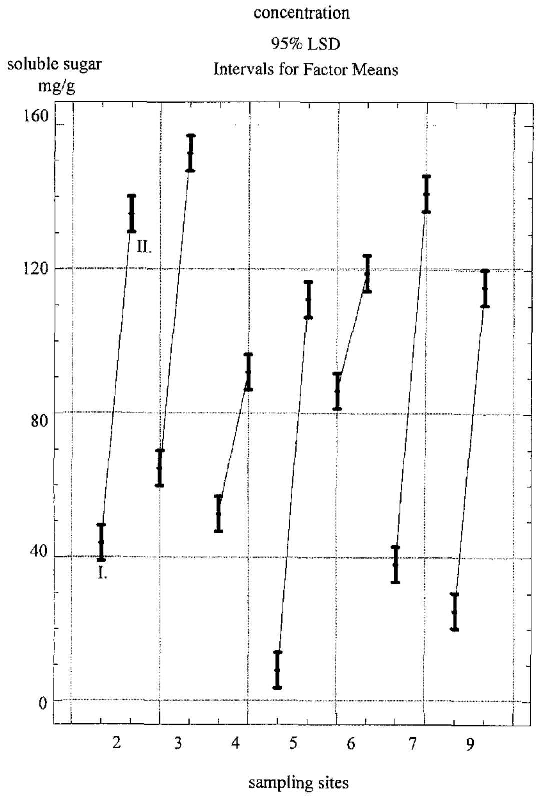
There were significant differences between the P concentrations of sampling sites 2, 4, and 5 (vigorous sites) in early summer. In that period the P concentration of the rhizomes was extremely high at sites 2 and 4. In autumn it was significantly low at sites 3, 5, 6 and 7 (Fig. 12).

The K concentrations of the sampling sites were compared only in early summer. There were no significant differences between sites 2, 4, 6 and 7, but at sitse 3, 5 and 9 significantly smaller K concentrations were measured (Fig. 13).

- Biomass and standing stock

The rhizome systems of die-back and vigorous reed stands differed from each other in the following characteristics:

- The average rhizome diameter was smaller at die-back than at vigorous sites (die-back site: 7.7–9.1 mm, vigorous site: 8.3–12.7 mm).



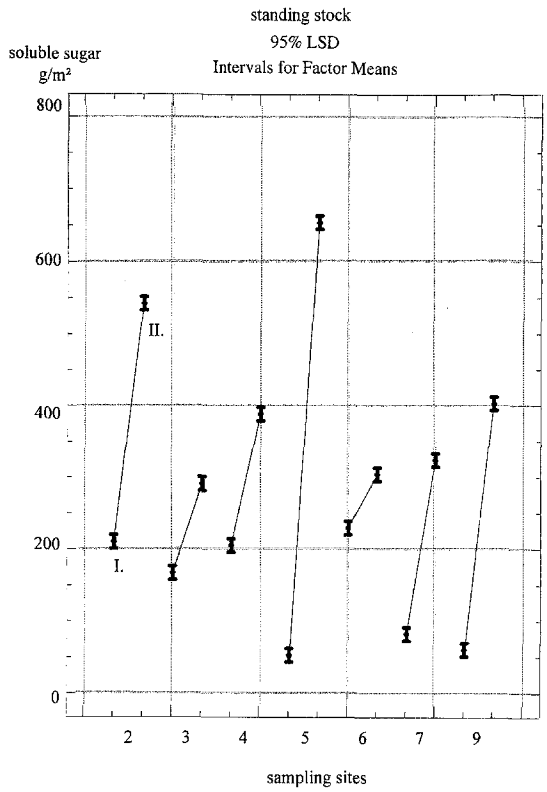
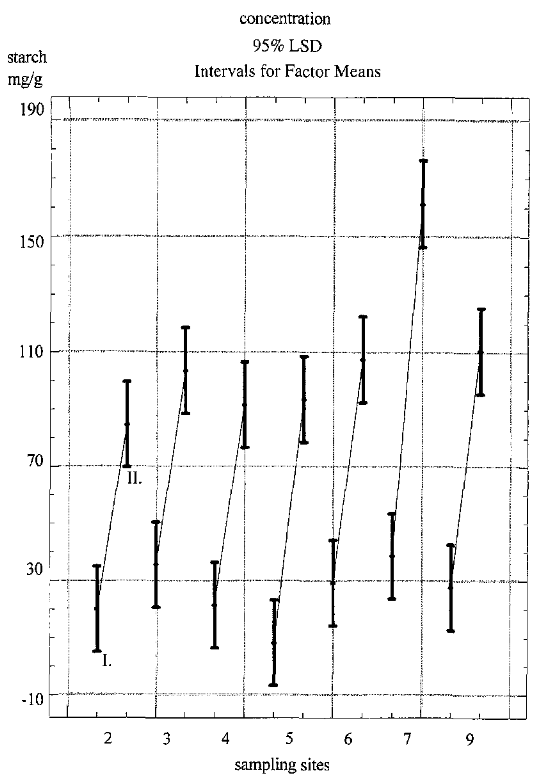


Fig. 8. Spatial comparison of the soluble sugar concentration and standing stock in the rhizomes. At all sites two means with the least signif cant differences are given. I: May 26, 1993; II: October 24, 1994. Vigorous sites: No. 2, 4, 5 and 9; die-back sites: No. 3, 6, 7.



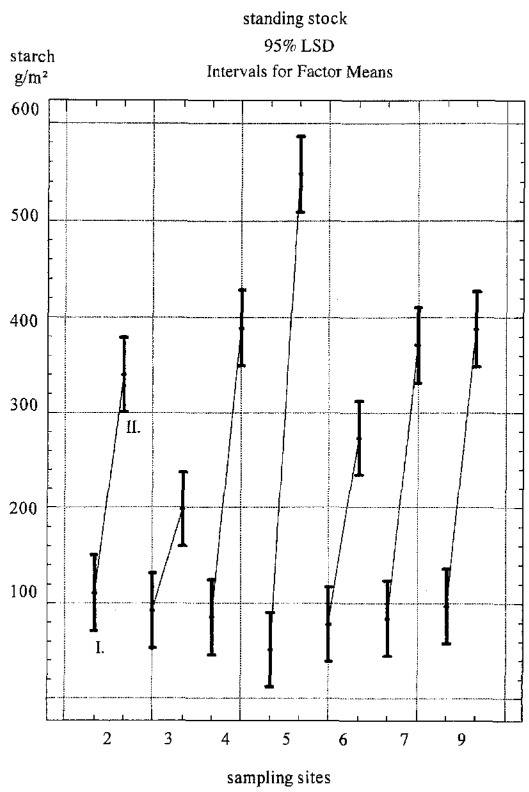


Fig. 9. Spatial comparison of the starch concentration and standing stock in the rhizomes. Explanations are as for Fig. 8.

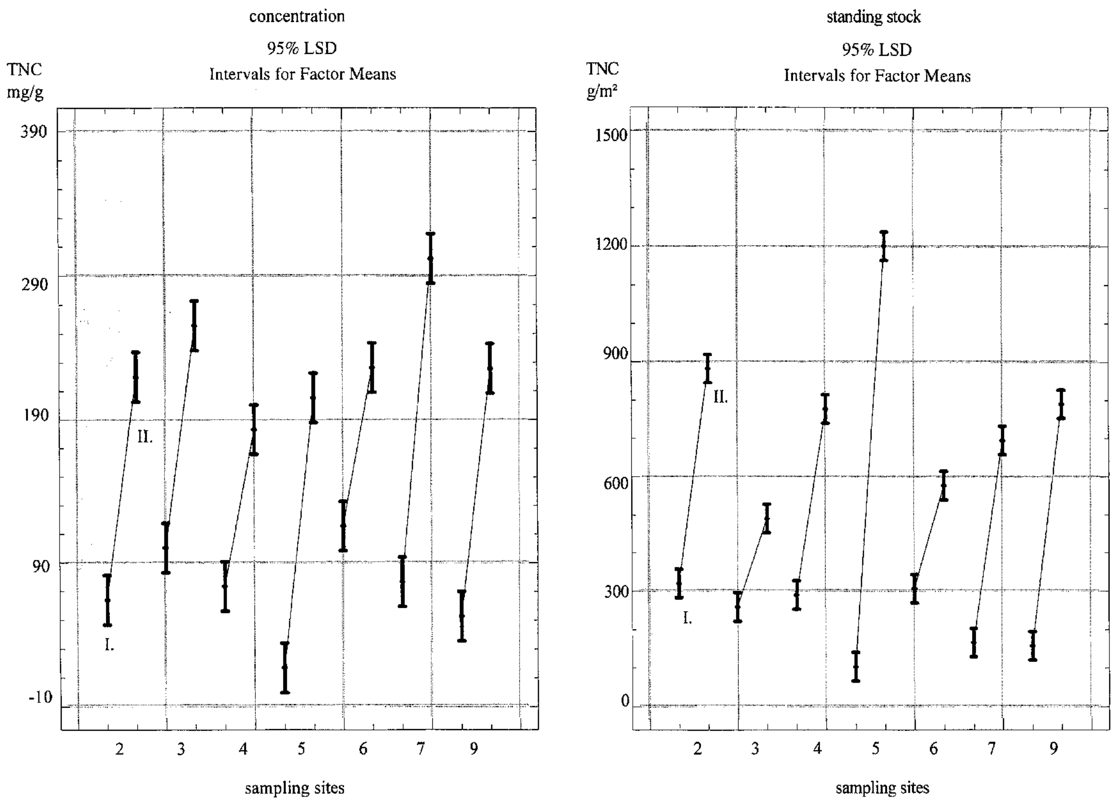


Fig. 10. Spatial comparison of the TNC concentration and standing stock in the rhizomes. Explanations are as for Fig. 8.

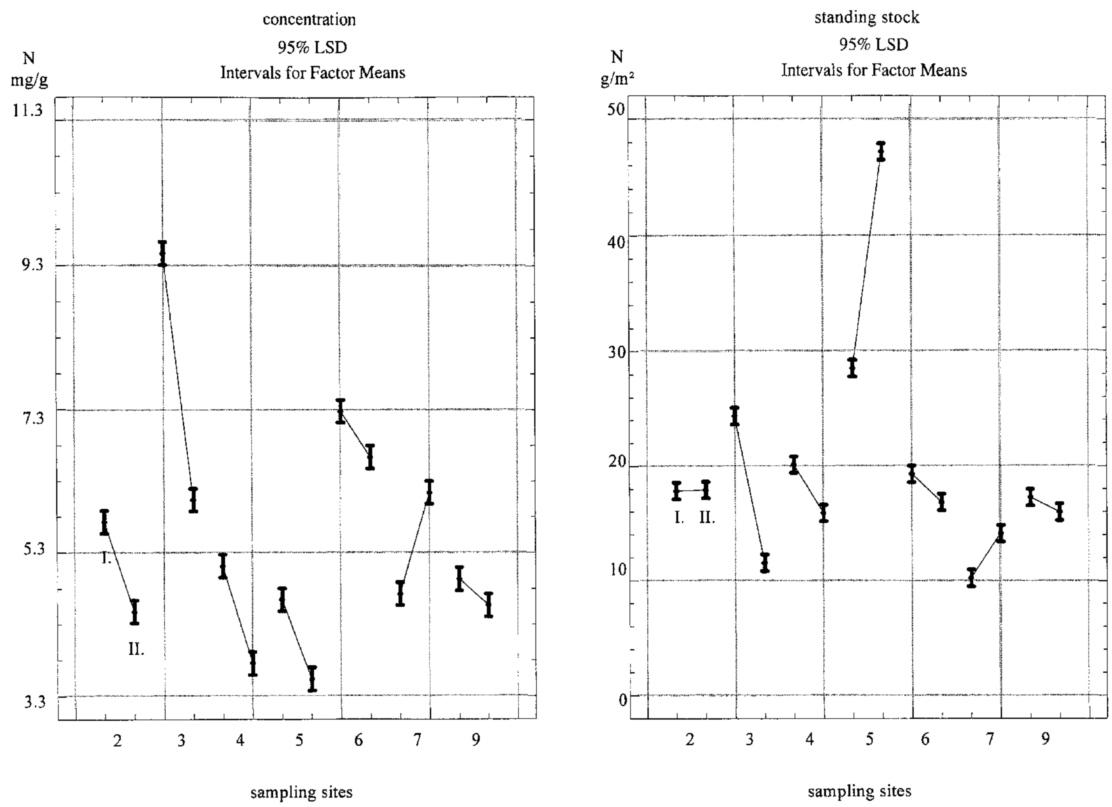


Fig. 11. Spatial comparison of the N concentration and standing stock in the rhizomes. Explanations are as for Fig. 8.

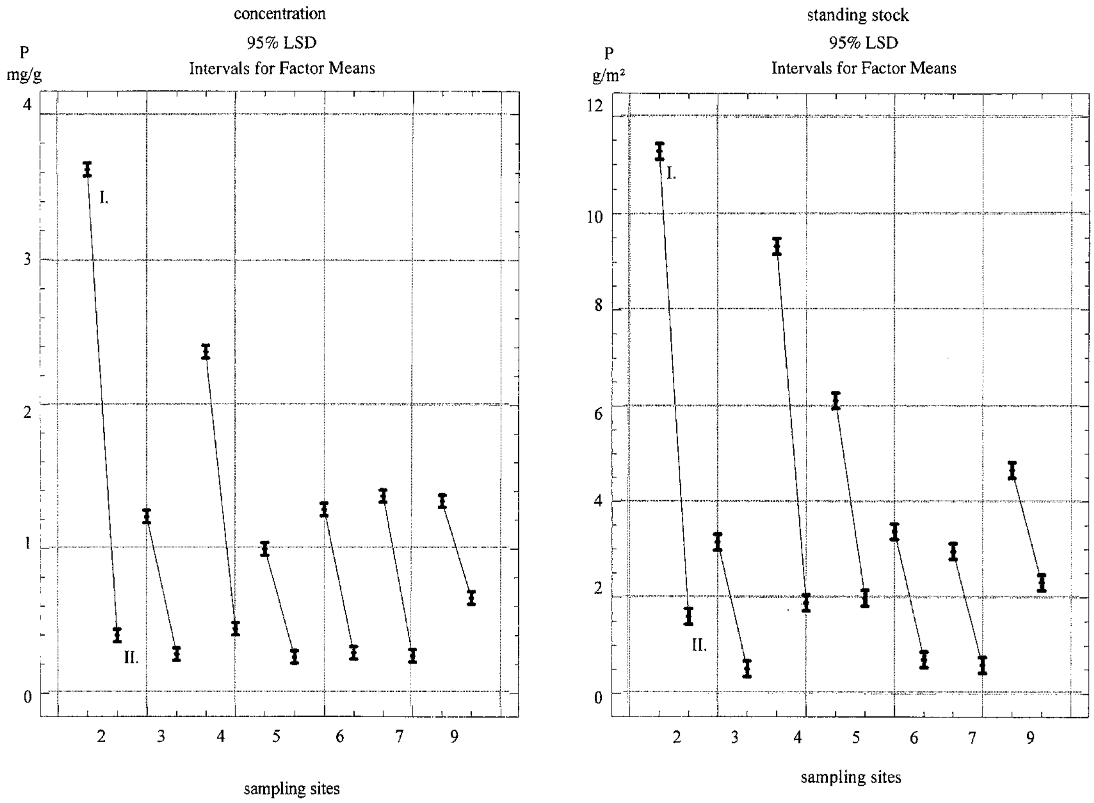


Fig. 12. Spatial comparison of the P concentration and standing stock in the rhizomes. Explanations are as for Fig. 8.

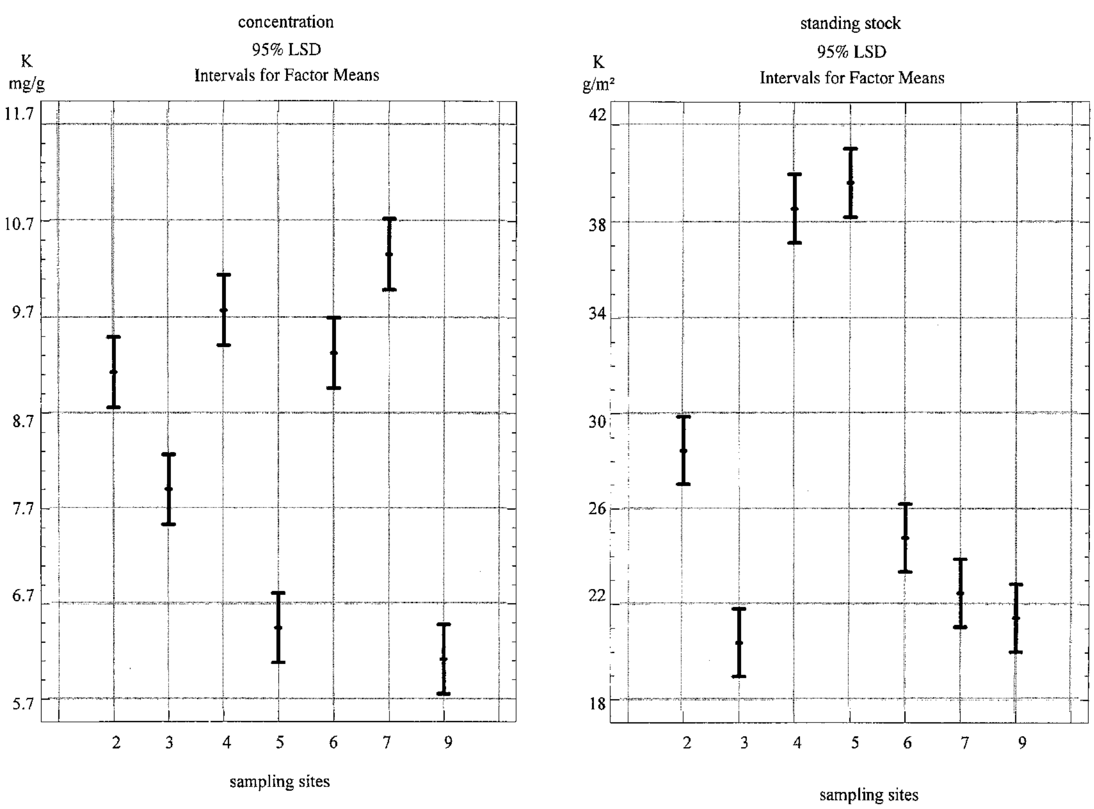


Fig. 13. Spatial comparison of the K concentration and standing stock in the rhizomes (only May 26, 1993).

- Only very young rhizomes were healthy in a die-back reed stand, rhizomes older than two years were deteriorated and insect-gnawed. While the apical part of the rhizome was growing in the vegetation period the basal part was often deteriorating. As a consequence, healthy rhizome parts could only be sampled if the youngest rhizomes were collected.

The average rhizome biomass was less at die-back (1900–2700 g/m^2), than at the vigorous sites (3100–6100 g/m^2). There were no significant differences between the rhizome biomass in summer and in autumn. Variation between replicates was relatively high compared to seasonal differences. The rhizome biomass was significantly higher at site 5 than at the die-back sites (3, 6 and 7). No significant differences were found between the other sites (Fig. 14).

The carbohydrate standing stock of the individual sampling sites showed a greatly different distribution pattern from those of the concentrations (compare Figs. 8, 9 and 10).

In early summer there were spatial differences both in the soluble sugar and the TNC standing stock of the rhizome, but the level of the starch standing stock was uniform. In this period the TNC and the soluble sugar standing stocks at sites 5, 7 and 9 were nearly the same, significantly lower than at the other sites. The situation greatly changed by autumn (compare Figs. 8, 9 and 10), when the soluble sugar, starch and TNC standing stocks were significantly the highest at site 5, a vigorous site with a high water cover. In autumn the carbohydrate standing stock was significantly lower at sites 3, 6 and 7 than at the vigorous sites (Fig. 10).

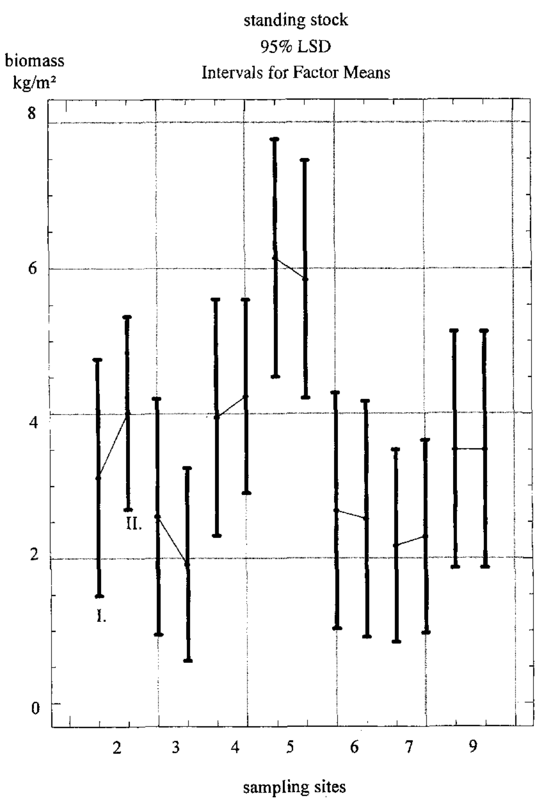


Fig. 14. Spatial comparison of the rhizome biomass. Explanations are as for Fig. 8.

In autumn there were considerably smaller soluble sugar standing stocks in the rhizomes at a given unit area at sites 3 and 6 (die-back sites) than e.g. at sites 2, 4, 5 and 9 (vigorous sites). Significant differences were found between the latter sites (Fig. 8).

In autumn the starch standing stock of the sampling sites was greatly different. The significantly highest values were measured at site 5, the significantly lowest values at sites 3 and 6 (both are die-back sites). The starch standing stock of the rhizomes was nearly the same at the other sites (340–380 g/m^2).

From the comparison of the mineral nutrient concentrations and standing stock of the different sampling sites in two different months (May 26, 1993; October 24, 1994) the following conclusion can be drawn: While the early summer and autumn N concentration was significantly the lowest (at site 5, a vigorous, deep-water covered reed stand) the N standing stock of the rhizomes was significantly the highest at the same site. The N standing stock of the die-back sites was significantly low (Fig. 11) especially in autumn.

The P standing stock of the rhizomes was significantly the lowest at the die-back sites both in early summer and autumn (Fig. 12). In summer the P standing stock of the vigorous sites (No. 2, 4, 5 and 9) differed significantly even from each other. In autumn their P standing stock was nearly the same, with the exception of site 9.

There were important differences in the K standing stock of the rhizomes at the individual sites in early summer (Fig. 13). The lowest K standing stock was found at the die-back sites (No. 3, 6 and 7) and at site 9, a vigorous reed bed (19.3–24.5 g/m^2).

5. Discussion

No important differences were found between the summer and autumn biomass of the rhizomes. In that period the rhizome biomass was relatively stable (Granéli et al. 1992). The spring rhizome biomass decrease is partly due to the translocation of the carbohydrate (Granéli et al. 1983, 1992; Fiala 1973, 1976; Hocking 1989), which is also indicated by the decrease of the TNC, starch and soluble sugar concentrations. The TNC concentration decrease can be up to 50% (Table 2). According to the literature no similar decrease has been recorded so far at any other site. The translocated carbohydrate is used up for shoot developement, respiration and mortality. This metabolic relationship also means that a decrease in the rhizome biomass sets an upper limit to the translocation of the carbohydrates from the rhizome to the shoot. In early spring (end of March) the number of 10 to 40 cm high, leafless shoots was 16 to 79% of the maximal number in the summer (Table 2).

The soluble sugar standing stock is low in the rhizomes in spring, but it gradually increases until autumn. Die-back and vigorous reed stands can be distinguished on the basis of their late summer soluble sugar standing stock. The autumn standing stock was lower in die-back reed stands (290–320 g/m^2) than at the vigorous sites (390–650 g/m^2; see Fig. 8). A good example was found at site 5, where the high water cover (1.2 m) exhausted the carbohydrate (sugar, starch, TNC) reserve of the rhizomes (see Fig. 5). Their concentrations were much lower than at the die-back sites. The general outlook of site 5 also differs from a typical vigorous site, reed is growing in groups and there are open water areas between the tussocks but the tussocks are so near to each other that this structure cannot be recognized in aerial photos. Reed degradation begins similarly e.g. at the open water edge of Lake Balaton, where reed stands are in deep water. As degradation processes go further the number of tussocks decreases, the open water area increases and the reed stand thins out. Tussock development is a strategy to survive in deep water, buds can start growing from a higher level and as a consequence they grow through only half or a third of the complete water cover.

Only the youngest parts of the rhizomes were intact, suitable for our investigation in die-back reed stands. In spring this was demonstrated with the high soluble sugar and starch concentrations at all die-back sites, and the high N concentrations at sites 3 and 6. Unlike vigorous reed stands, where three and four year old rhizomes are still functioning (FIALA 1976; GRANÉLI et al. 1992), at die-back sites only the one or two year old parts are healthy. The annual rhizome mortality is 30% in vigorous reed stands, it reaches or sometimes even exceeds, 50% at die-back sites, where half or an even greater proportion of the rhizomes can die off (DINKA et al. 1995).

If there is a large amount of rotting organic matter in the sediment, it promotes the development of unfavourable conditions for reed. Anaerobic conditions deprive the rhizomes of oxygen causing hypoxia, especially during winter dormancy when pressurised influx of oxygen through the leaves and stem is interrupted (ARMSTRONG et al. 1988, 1995 a). Hypoxia can also develop during the summer if the stem is damaged and the bore decreases the efficiency of venturi and convective oxygen transport, or callus develops on the rhizome or on the roots. ARMSTRONG et al. (1995 b) found the latter process to be more intensive in die-back than in vigorous reeds. It is caused by the increased sulphur-hydrogen concentration of the sediment due to anaerobic conditions (die-back sites: 50–150 ppm, vigorous sites: 4–20 ppm). In other areas the presence and unfavourable phytotoxic effects of volatile organic acids formed during the anaerobic rotting of the organic matter content in the sediment has been described by KOVÁCS et al. (1989).

In most comparisons the carbohydrate concentrations measured in our investigation were lower than in other studies (FIALA 1973, 1976; GRANÉLI 1983, 1992; HALDERMANN & BRÄNDLE 1986; ČIŽKOVÁ et al. 1995; KUBIN et al. 1995), but BEST et al. (1989) reported even lower values.

The P and K concentrations in the rhizomes were generally lower in our studies than in another investigations at Lake Fertõ/Neusiedlersee (SIEGHARDT et al. 1984). There is no obvious explanation for these differences.

Similar annual N, P and K concentration dynamics were recorded in the reed rhizomes by KVĚT (1973), DYKYJOVÁ & HRADECKÁ (1976), HO (1981), DINKA (1986) and HOPKINS (1989).

The carbohydrate and nutrient concentrations, as well as standing stocks in the reed rhizomes at different sampling sites of Lake Fertõ/Neusiedlersee have been compared in the present paper. The concentrations were higher in die-back reeds at the beginning of summer and in autumn, the standing stocks were higher at the vigorous sites. It is of special importance for resistance to unfavourable effects at die-back sites.

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